THE REACTION OF *VIMINARIA DENUDATA* TO INCREASED WATER CONTENT OF THE SOIL.

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(Plate xxii; eighteen Text-figures.)

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Introduction.

The observations given below are put on record in the hope that they may be of use in the interpretation of some of the anatomical peculiarities of marsh and water plants. A description is given of the reactions of the shrub, *Viminaria denudata* Sm., to a great increase in the water content of the soil in which it is growing; and also a brief consideration of the theoretical conclusions to be deduced from its behaviour.

Viminaria denudata Sm. belongs to the subfamily Papilionaceae of the Leguminosae. It is a switch plant attaining a height of about 12 feet. True leaves are present only in the juvenile stage, their function being early assumed by phyllodes which are terete, up to 15 inches long, and fairly firm but not rigid. It is interesting on account of the unusual degree of plasticity shown in its reaction to a change of environmental conditions. On the whole *Viminaria* requires a relatively moist soil for its best development.

In the Sydney (N.S.W.) district the geological formation is Mesozoic; three series of rocks, Narrabeen Beds (sandstone and shale), Hawkesbury Sandstone, and Wianamatta Shale, are present. In country where the soil is derived from sandstone rocks, *Viminaria* is limited, in most cases, to the banks of streams. But where the soil comes from weathered shale, and consequently has a higher water retaining capacity, *Viminaria* is often found in moderately sheltered positions remote from running water, even on slopes and hilltops. It is also quite commonly present along the margins of both freshwater and brackish swamps.

Some *Viminaria* shrubs which came under observation grew on the banks of a stream in sandstone country; the soil there was porous and usually damp, but not saturated. From 17th June to 5th July, 1930, steady rain fell, a total of 870 points being recorded. This caused the stream near which the *Viminaria* grew to overflow its banks, and the ground nearby became thoroughly saturated, and in places was under as much as six inches of slowly flowing water. The *Viminaria* plants remained in a flourishing state throughout the flooding. Their most conspicuous reaction to the change was the production by their roots, of short white breathing roots or pneumatophores. The photograph reproduced in Plate xxii, fig. 1, shows a small part of the flooded ground, and a number of the pneumatophores can be seen rising above the surface of the water amongst seedling plants and clumps of reed. Since then pneumatophores have frequently been observed on plants growing in temporarily saturated soils. The reaction to the flooding is very rapid, and recognizable pneumatophores may be produced in three or four days.

Viminaria may also show another feature characteristic of some marsh plants when its root system remains submerged for a week or more. This is the production of secondary aerenchyma. In the case of plants which grow near swampy ground, secondary aerenchyma is regularly developed. But it is important to notice that pneumatophores are not produced by these plants unless the soil is quite saturated.

General Description.

a. *Pneumatophores.*

i. Habit.

The root system of *Viminaria* is mainly shallow, whether the plant grows in moist or in wet soils. There are, as a rule, three or more main roots which grow practically horizontally at a depth of one to four inches below the surface of the soil. These roots give rise to branches of various sizes. The smaller ones ramify in all directions and are probably the main absorbing organs of the plant. The larger ones keep a more or less horizontal course, giving rise in their turn to smaller roots. Large *Viminaria* plants, especially those growing in well aerated, sandy soils, usually also have some deeply penetrating roots.

As previously stated, pneumatophores are produced by a root system of *Viminaria* when the soil in which it is growing becomes saturated. These pneumatophores are roots of spongy appearance and brittle nature, which develop from the beginning under almost aquatic conditions. In consequence they have, when mature, a structure quite different from that of roots which grow in well aerated soils. In habit they resemble to a remarkable degree the pneumatophores produced by some mangroves, though they lack the pneumatothodes present in those types.

Classified on their habit, the pneumatophores of *Viminaria* are of two kinds, (1) upright, and (2) "knee-bend"; and according to their mode of origin, the upright pneumatophores can be further divided into two classes, (*a*) primary, and (*b*) secondary.

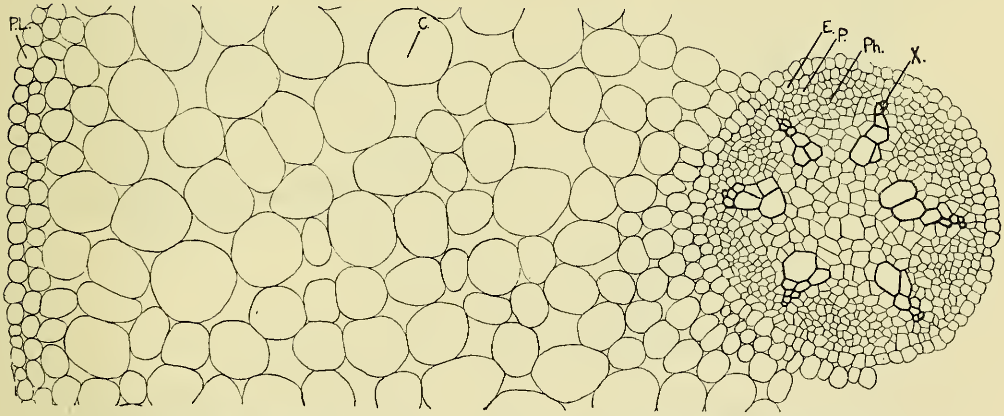
For the production of a primary upright pneumatophore the growing point of a horizontal root turns and grows upwards above the surface of the soil or water. When there is a length of 0·5 to 6 cm. of root projecting into the atmosphere, growth ceases, the root-cap curls up and drops off, and various changes which will be discussed below, take place in the internal anatomy. The central pneumatophore (P) in Plate xxii, fig. 4, is a primary one, which has been broken off above the bend. Primary pneumatophores do not seem to be very common, the great majority of upright roots being secondary ones.

Submerged horizontal roots give rise to laterals corresponding to the absorbing roots of plants growing in damp soil. If these laterals arise from the under side of the root, they grow out and downwards, and act as absorbing roots (Plate xxii, figs. 2 and 3, A). But those which originate from the upper side grow vertically upwards into the air, forming secondary upright pneumatophores which are indistinguishable superficially from primary ones. Plate xxii, figs. 2, 3 and 5, show upright secondary pneumatophores arising from horizontal roots.

Mature pneumatophores occasionally produce lateral roots which also grow upwards into the atmosphere. This seems to be especially characteristic of the primary type. Plate xxii, fig. 4, shows the upper part of a primary pneumatophore with eight laterals growing up around it. In Plate xxii, fig. 5, the secondary upright root at the extreme right has produced one young lateral. Absorbing roots are also occasionally produced at the bases of primary and secondary pneumatophores.

The upright pneumatophore functions for a week or longer after reaching its full size; it then begins to wither away from the tip (see upright pneumatophores in Plate xxii, fig. 2), but the part under water still remains alive for a variable time. Should the water level recede after flooding, the upright roots collapse and die, since their delicate and unprotected tissues are unable to withstand desiccation. If, on the other hand, the water level should rise still further after an initial flooding, a mature pneumatophore cannot grow and keep pace with it, having lost the power of apical development. Under such circumstances it may give rise to secondary pneumatophores which grow up above the new water level.

The second kind of pneumatophore, the "knee-bend" type, resembles in habit the breathing roots of the mangrove *Aegiceras*. It occurs exclusively as a modification of a horizontal root. Though by no means as common as the upright roots, this form is quite frequently met with, and seems to be commoner in saturated soils than water. For its formation, a horizontal root commences to grow upwards as if to form an upright root. But when it reaches the atmosphere, instead of continuing its upward course, the growing point turns and grows down again into the soil and there continues its original direction of growth (Plate xxii, figs. 2 and 3, K).



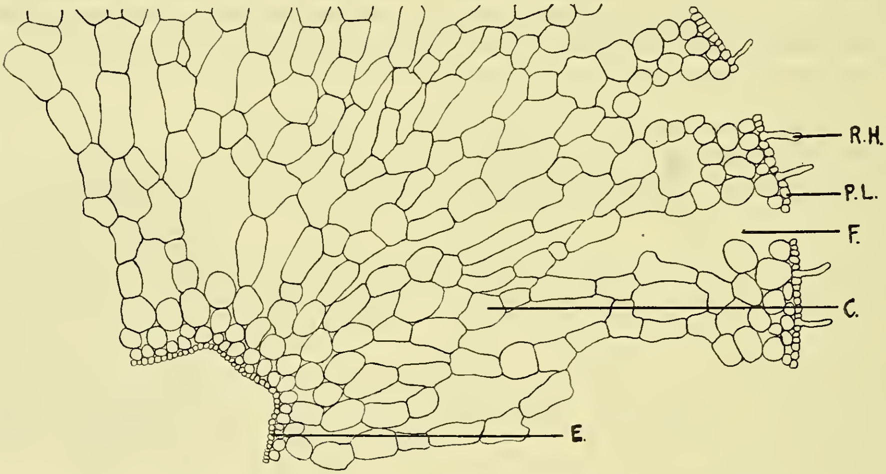
Text-fig. 1.—Transverse section of a young root which has developed in a saturated soil. P.L., piliferous layer; C, cortex; E, endodermis; P, pericycle; X, xylem; Ph., phloem. × 150.

Several "knee-bends" are occasionally found close together on the same root, and it is a frequent thing for a horizontal root to give rise to both upright and "knee-bend" pneumatophores. Several cases were observed (Plate xxii, figs. 2 and 3) in which an upright pneumatophore grew out from the top of a "knee-bend". It is likely in this case that, after the formation of the "knee-bend", a second flooding submerged it and stimulated the development of the upright root.

ii. Internal anatomy.

Text-figure 1 shows part of the transverse section of a young upright pneumatophore at about the stage of the three at the left of Plate xxii, fig. 5. The structure is that of a typical dicotyledonous root. There is the usual central stele with 4- to 9-arch xylem, an unthickened endodermis and a fairly wide primary cortex of large rounded cells. A noticeable feature of the cortex is the presence of an unusually well developed system of intercellular spaces, especially in the middle cortex. The piliferous layer and one or two layers of cells below it are composed of smaller cells, and this band forms a fairly compact region on the outside of the young root. A young absorbing root, and the first 2 to 6 centimetres of a horizontal root show, in transverse section, features essentially similar to those described for the young upright pneumatophore. Pneumatophores and horizontal roots subsequently become much modified, but an absorbing root retains this structure throughout its period of primary growth; only in one case was an absorbing root found which had developed a little aerenchyma at its base, and since this was similar to the tissue regularly developed by pneumatophores, it will not be described separately.

In sections of slightly older pneumatophores, it is seen that the cells of the cortex have increased to as much as three times their original diameter in a radial direction. The intercellular spaces between them increase in both radial and tangential directions (see Text-figs. 2, 3). This increase is most marked in the middle cortex, where the cells pull apart and often assume X and Y shapes, with only the ends of the arms in contact. The cells of the compact outer layer do not increase much in size, and have evidently lost the power of division. This layer therefore becomes ruptured in numerous places by the pressure exerted by the extending cells below. These breaks often extend as fissures deep into the cortex. This process of aerenchyma formation proceeds gradually upwards from the base of a root towards the tip, and in mature pneumatophores air-spaces are present right to the apex, and the root-cap has broken away.

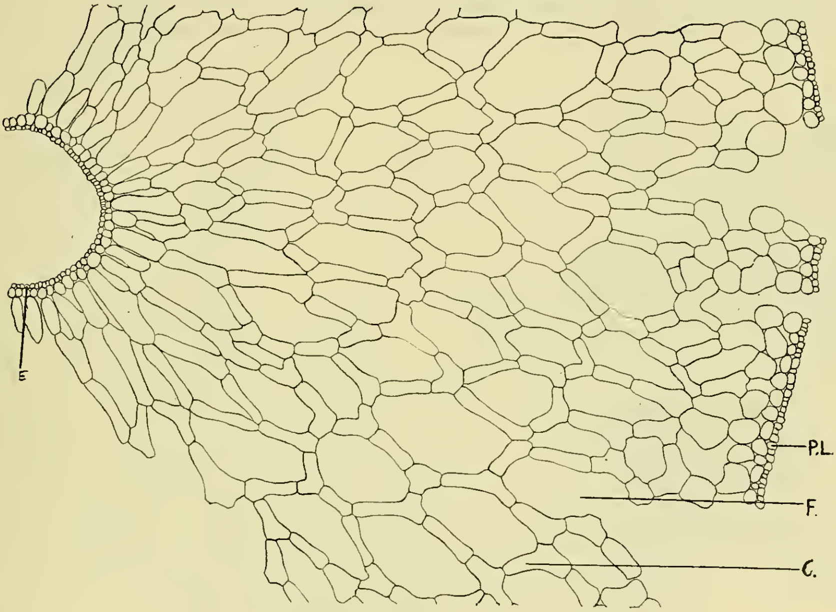


Text-fig. 2.—Transverse section of a young pneumatophore at a slightly more advanced stage than shown in Text-fig. 1. P.L., piliferous layer; R.H., root hair; F, fissure in tissue of cortex (C); E, endodermis. × 50.

Text-figure 2 shows an early stage in the development of aerenchyma in the young pneumatophore, the cortical cells have begun to extend, and the intercellular spaces are already quite large. A number of narrow fissures (F) are shown, and root hairs of a rudimentary appearance are present. A section 3·5–6 cm. from the apex of a horizontal root would show a structure similar to this.

Text-figure 3 is part of a transverse section of a mature pneumatophore; it shows the final stage in the development of primary aerenchyma in the cortex.

A mature upright pneumatophore is 0·5–1 cm. in diameter at its widest part, tapering towards the apex and often slightly towards the base also. Plate xxii, fig. 4, shows this feature well. In Plate xxii, fig. 5, the young pneumatophores on the left are still in the first stage of development, whilst the four at the right are mature and taper towards both base and apex. The horizontal roots remain of constant diameter (about 0·5 cm.), except towards the growing point, until the commencement of secondary growth (Plate xxii, fig. 5). The fissures seen in transverse section in the mature pneumatophore are visible externally as narrow slits of varying length (Plate xxii, figs. 3, 5).



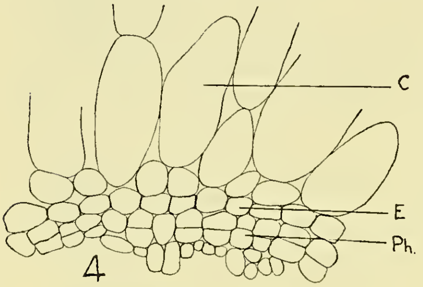
Text-fig. 3.—Transverse section of a mature pneumatophore. P.L., piliferous layer; F, fissure in tissue of cortex (C); E, endodermis. × 40.

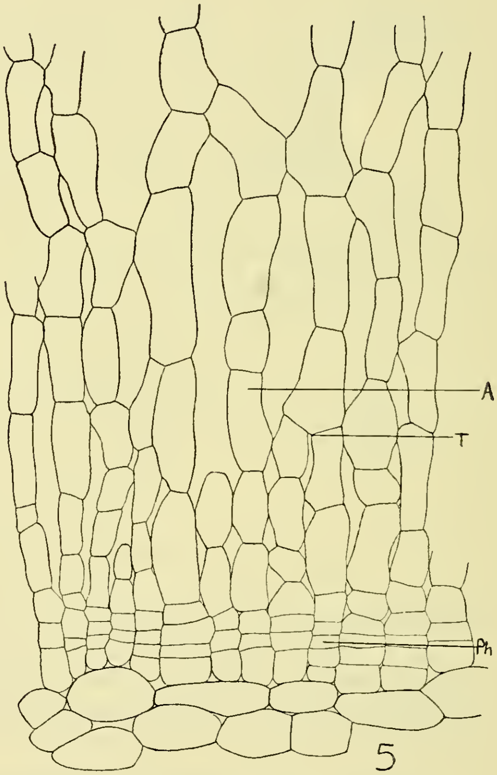
b. *Secondary Aerenchyma.*

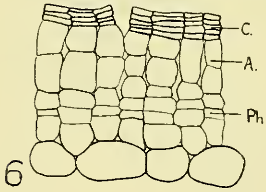
The upright pneumatophores and the larger "knee-bends" undergo no further development and finally die away, but secondary growth takes place in horizontal roots, and in those producing "knee-bends" so short that they only reach the surface of the ground and do not come above it.

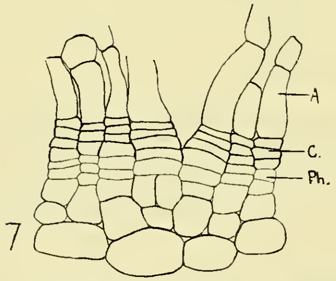
Soon after cambial activity commences in the stele, a phellogen arises in the cells of the pericycle. Text-fig. 4 shows the first divisions taking place in the pericycle. When the soil in which the root is growing is moderately dry, cork cells are cut off externally in the usual way. But when the ground is flooded, cells are cut off externally whose walls remain unsuberised. These cells increase in length in a radial direction forming a secondary aerenchyma (Text-fig. 5, A). As a rule very little phelloderm is present, even in old roots.

As the central stele enlarges with the addition of secondary xylem and phloem, pressure is exerted on the phellogen. This pressure causes the cells of the phellogen to stretch in a tangential direction (cf. tangential diameter of the cells of the phellogen in Text-fig. 4 which is very young, with those in Text-fig. 5 which are much older) till finally the secondary aerenchyma cells cut off by them are not a great deal narrower than the cells of the primary aerenchyma. Once the cells of the phellogen have reached a maximum width, further increase in the size of the stele must be accommodated by tangential divisions in the phellogen.









Text-fig. 4.—Portion of a transverse section of a horizontal root including the pericycle, endodermis (E), and the innermost layers of the primary cortex (C). The phellogen (Ph.) is shown arising in the pericycle. × 150.

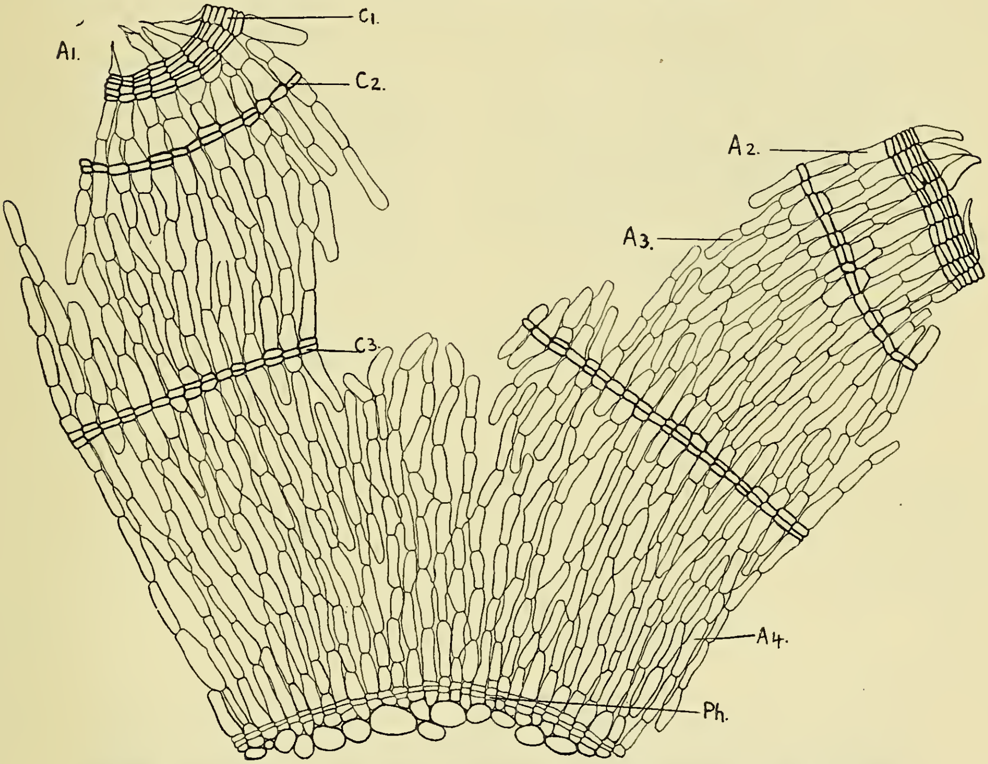
Text-fig. 5.—Portion of a transverse section of an old horizontal root showing the secondary aerenchyma (A), arising from the phellogen (Ph.). × 150.

Text-fig. 6.—Portion of a transverse section of an old horizontal root showing the development of secondary aerenchyma (A) below a layer of cork (C). Ph., phellogen. × 150.

Text-fig. 7.—Portion of a transverse section of an old horizontal root showing the development of a thick layer of cork (C) below secondary aerenchyma (A). Ph., phellogen. × 150.

The cells in Text-fig. 5 are of full size and there is evidence of a tangential division having taken place at T. The cells cut off externally by the phellogen evidently elongate at once in a radial direction with great rapidity. Evidence of this is found in the small number of cells intermediate in size between those of the phellogen and the aerenchyma.

The primary cortex and the outer secondary aerenchyma are pushed out, die and become brown, and fissures arise which are longer, deeper and more irregular than those of the primary pneumatophore. Usually they appear as winding furrows 3–5 cm. long; more rarely they are short and straight.

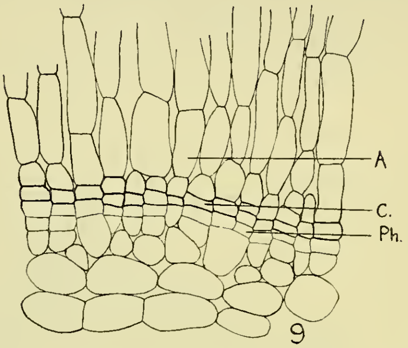


Text-fig. 8.—Portion of a transverse section of the periderm of an old root showing the development of successive rings of cork of varying widths, and a large fissure. C1, C2, C3, successive rings of cork; A1, A2, A3, A4, successive bands of aerenchyma; Ph., phellogen. × 40.

The cells of the secondary aerenchyma on the whole are slightly smaller than those of the primary cortex and, though they are arranged in regular rows end to end, there are fewer radial points of contact, so that the tissue as a whole is much less compact.

It is evident that the formation of aerenchyma is dependent on the saturated condition of the soil, since flooding induces the formation of aerenchyma in old roots which had already developed a layer of cork when growing under conditions of better soil aeration. Text-fig. 6 shows a band of cork being thrust outwards by the development of thin-walled cells below it. Then again, when the soil becomes relatively dry after flooding, a band of cork is formed in roots which previously may have developed only secondary aerenchyma. In Text-fig. 7 the secondary aerenchyma is shown in the process of being cut off by a cork layer; it is in consequence brown and dead.

One feature of the aerenchyma of some of the large horizontal roots is of particular interest as evidence of the extreme rapidity with which the plant reacts to a change in its environment; a puzzling condition was met with in sections of roots which had a large amount of secondary aerenchyma. At varying intervals the aerenchyma tissue was interrupted by layers of cork cells 1–8 or more cells in width (Text-fig. 8); their walls were evidently suberised, since they stained deeply in chlor-zinc iodine, strong caustic potash, and Sudan III. It is a very conspicuous feature that there is little or no gradation either in the size of the cells comprising the two types of tissue, or in the amount of suberisation of their walls. The transition from one type of tissue to the other is extremely abrupt.



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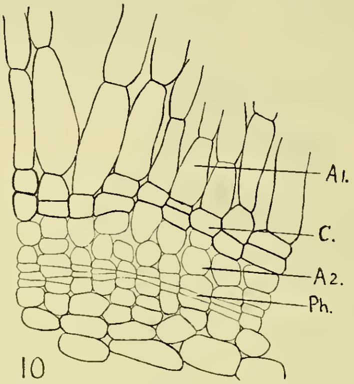

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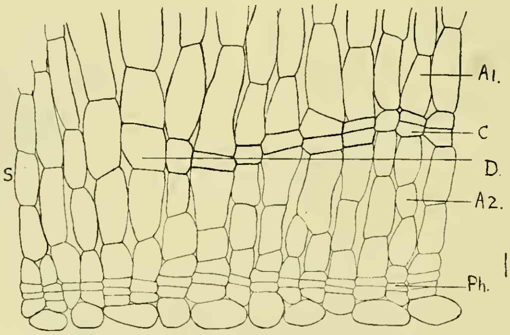

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Text-fig. 9.—Portion of a transverse section of the periderm of an old horizontal root. A cork layer (C) has just been cut off from the phellogen (Ph.). A, secondary aerenchyma. × 150.

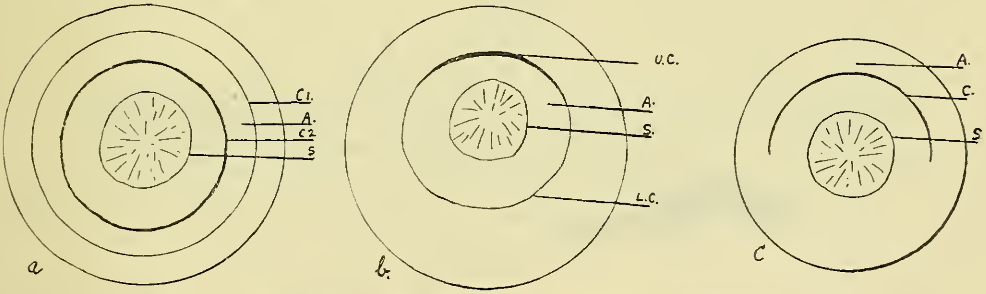
Text-fig. 10.—Portion of a transverse section of the periderm of an old horizontal root, showing the formation of aerenchyma (A2) below a cork layer (C). Ph., phellogen; A1, old secondary aerenchyma. × 150.

Text-fig. 11.—Portion of a transverse section of the periderm of an old horizontal root showing the abrupt ending off of a cork layer at D. S, under side of root; A, secondary aerenchyma; C, cork layer; Ph., phellogen. × 150.

Text-figure 9 shows a cork band which has just been cut off from the phellogen, and is already suberised. Text-figure 10 shows the resumption of aerenchyma formation after a band of cork has been formed; at this stage the previously formed aerenchyma is already dead. Text-figure 8 is part of a transverse section of a wide periderm, and it shows a number of interesting features. There are three cork layers in the part shown; C2 and C3 are narrow, but C1 is nearly as wide as the cork formed on roots which have developed from the beginning in well aerated soil. Moreover these three layers are placed at very uneven distances apart. The aerenchyma zone A4 is so wide that it is already beginning to die from the outside, while A3 is much narrower, and A2 is narrower still.

The distance between two cork rings is usually constant all the way round the root in any particular section (Text-fig. 12*a*), but occasionally one finds that the amount of aerenchyma between two cork layers is greater on the under side than on the upper, and where this is so, the part of the cork layer around the upper side of the root is slightly thicker than that around the lower side (Text-fig. 12*b*). The transition from the narrow to the wide part may be gradual or sudden. Text-figure 13 is part of a transverse section of some periderm tissue showing a sudden transition; cork is still being formed on the upper side of the root, while aerenchyma is still being cut off on the lower side (S). In Text-figure 10, S indicates the under side of the root; the cork layer C which is continuous over the upper half dies out at about D, and there is uninterrupted aerenchyma on the under side of the root (see also Text-fig. 12*c*).

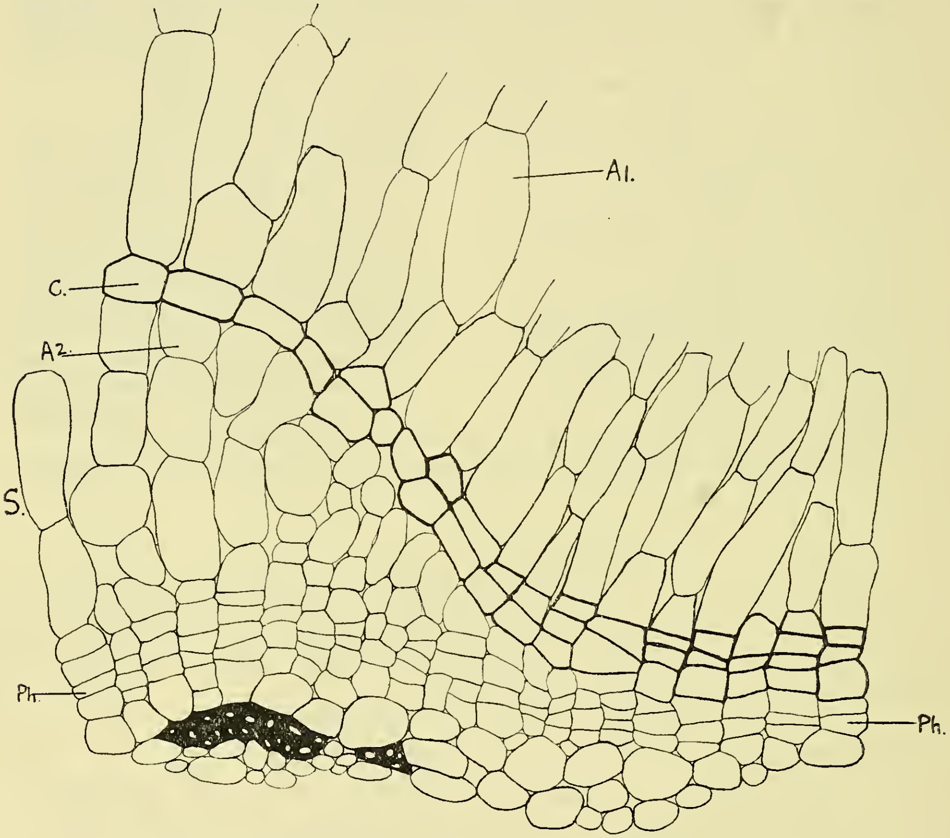
The significance of these cork layers and their irregularities will be discussed later.



Text-fig. 12.—Diagrammatic representations of the transverse sections of old horizontal roots illustrating the development of cork rings. 12*a* shows concentric rings of cork C1 and C2 around the central stele (S); A, secondary aerenchyma.—12*b* shows a ring of cork which is much thicker on the upper side (U.C.) than on the lower side (L.C.). The aerenchyma (A) is thicker on the under side of the root, both inside and outside the cork ring. 12*c* shows a discontinuous ring of cork, over the top of the root only. These figures are, of necessity, much simplified.

c. *Bunches of Secondary Roots.*

Another feature probably to be associated with saturation of the soil is the development on young growing roots of bunches of secondary roots (see Plate xxii, fig. 4, S). They are usually found just below the level of the ground, sometimes pushing through to the surface, and a thorough search revealed their presence only in water-logged and submerged soil. They consist of many hundreds of small secondary roots which arise on a length of young growing root of usually not more than 5 centimetres. They are thin and unbranched, with small growing points, and have numerous root hairs. The growth period of these roots is very limited; having attained their maximum length of about 2 centimetres they evidently function for a week to ten days and then die and rot away, leaving little trace on the exterior of the root which bore them.



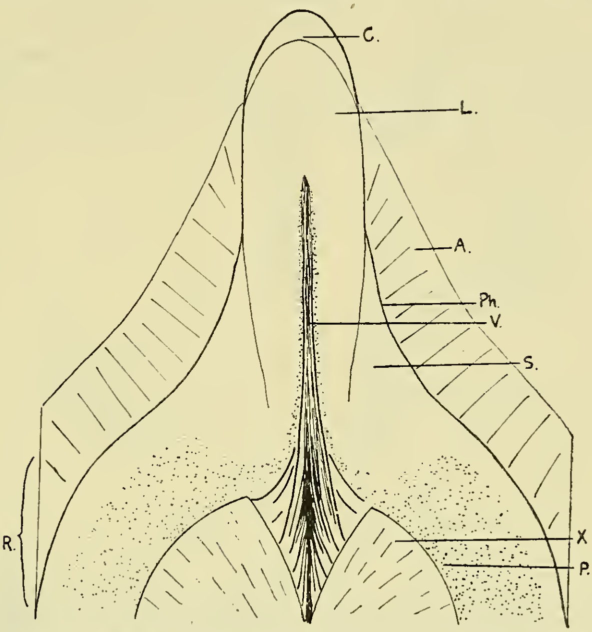
Text-fig. 13.—Portion of a transverse section of the periderm of an old horizontal root showing the resumption of aerenchyma formation under a narrow band of cork (C) on the lower side (S) of a root, whilst cork is still being formed by the phellogen towards the upper side. Ph., phellogen; C, cork layer; A1, old aerenchyma; A2, newly formed aerenchyma. × 200.

Their function remains obscure; it may be that they are organs of aeration similar in function to the pneumatophores, as their occurrence near to the surface of wet soil suggests. No trace of bacteria or fungi could be found in their tissues, and it is believed that their production is not due to stimulation by an endophyte.

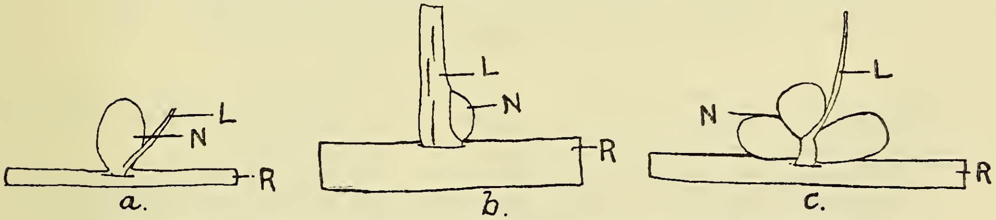
d. *Bacterial Nodules.*

In *Viminaria* bacterial nodules arise in one of two ways.

(1). Frequently young lateral roots arise from old roots which have already developed a fairly thick periderm; in the neighbourhood of the young root the phelloderm is very much wider than elsewhere. The periderm is pushed up round the young root as it emerges from the old root, and forms a collar 2–3 mm. high around its base. Text-figure 14 represents diagrammatically a transverse section through part of an old root showing the emergence of a young root and the upward extension of the periderm around it. A very usual place for bacterial infection is in the phelloderm of this upward extending region (S in Text-fig. 14); the actual point of infection is probably the cortex of the young root above the phellogen, and the infection thread of bacteria probably travels down from there into the phelloderm, since it is unlikely that infection could take place across a thick layer of aerenchyma which frequently includes bands of cork. A nodule then develops, covered from the beginning by an active phellogen which, under conditions of soil saturation, gives rise to an extensive secondary aerenchyma.

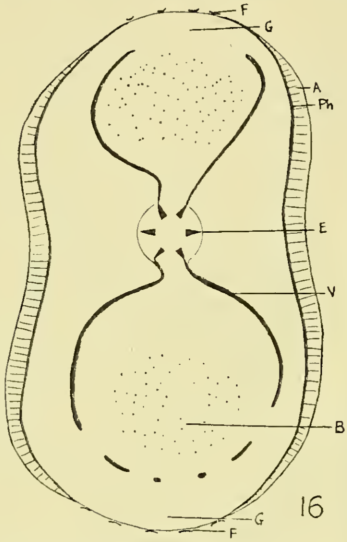


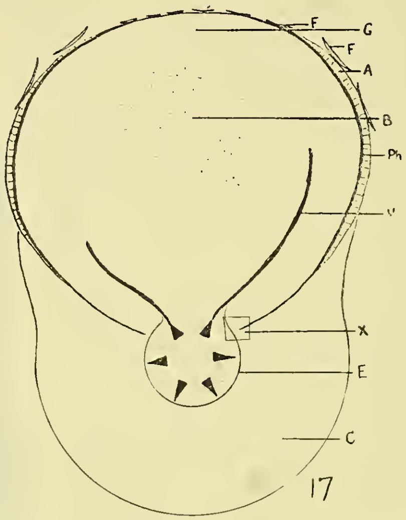
Text-fig. 14.—Transverse section of an old root (R) showing the departure of a young lateral root (L). X, secondary xylem of main root; P, phloem; Ph., phellogen; A, secondary aerenchyma; V, vascular strand of lateral root; G, root cap of lateral root; S, phelloderm.



Text-fig. 15.—Shows the formation of bacterial nodules (N) at the base of a lateral root (L). R, main root. *a*, *c*, × 1; *b*, × 2·5.

The nodule, very soon after its initiation, develops vascular strands which become linked up with the vascular tissue of the young root. Text-figures 15*a* and 15*b* show nodules at the base of young lateral roots, and Text-figure 16 shows diagrammatically a transverse section through the base of a young root which has two nodules within a common periderm. In the region of the growing point of the young nodule the phellogen loses its characteristic appearance and grades into the meristem region which consists of smaller, more isodiametric cells.





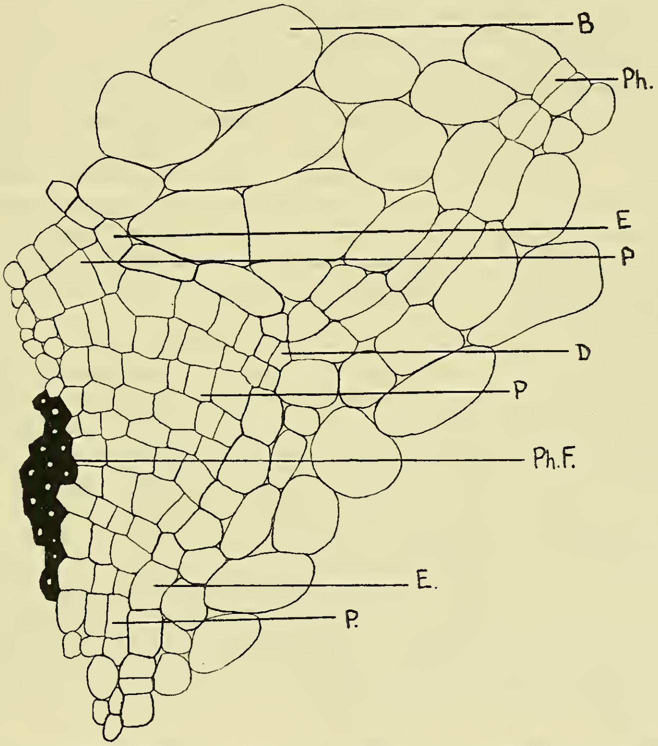
Text-fig. 16.—Transverse section of the base of a young lateral root showing the development of two nodules within a common phellogen. V, vascular strands to nodules; E, endodermis; A, secondary aerenchyma; Ph., phellogen; F, isolated fragments of aerenchyma pushed out by the growth of the nodules; G, growing point of nodule; B, bacterial region.

Text-fig. 17.—Transverse section of a young root, showing the second method of nodule formation. E, endodermis; A, secondary aerenchyma; Ph., phellogen of nodule; V, vascular strands to nodule; F, isolated fragments of primary aerenchyma; G, growing point of nodule; B, bacterial region; C, cortex of root; X, portion shown enlarged in Text-fig. 18.

Frequently, as shown in Text-figure 16, two or more nodules may commence to grow within a common periderm, and a large lobed nodule is finally formed at the base of the lateral root. This root never, apparently, reaches any great size, but soon dies back leaving a group of nodules whose mode of attachment to the root system is at first quite obscure (Text-fig. 15*c*).

(2). In the second case the bacterial nodule commences in the usual manner after infection of the cortex of a young root. Cortical cells in the neighbourhood of the endodermis divide rapidly, pushing back the outer cortex. Very early in the formation of a nodule, usually before it has burst through the cortex, the cells around its edges begin to divide at right angles to its direction of growth. These peripheral cells are already much elongated by pressure exerted by the dividing cells within, and the new walls are laid down along their greatest diameter.

In this way a peripheral cambium zone is formed which, as soon as the nodule is free from the cortical tissues of the parent root, cuts off a secondary aerenchyma outside it. This dividing tissue is best regarded as a phellogen. It extends gradually down to the endodermis of the parent root, and finally joins up with a pericyclic phellogen developing later in the root. Text-figure 17 shows how this is accomplished. A phellogen arising in the pericycle of the root cuts off a considerable tissue of thin-walled cells, pushing out the endodermis in a position just below the phellogen of the nodule; a few cells of the endodermis lying between the two then divide tangentially, joining up the internal and external phellogens. Subsequently formed aerenchyma then clothes root and nodule without a break.



Text-fig. 18.—Enlargement of square marked X in Text-fig. 17, to show the linking up of the phellogens of the root and the nodule by the division of endodermal cells at D, between the two. E, endodermis; Ph., phellogen of nodule; B, base of nodule; P, pericycle of root dividing to form a phellogen; Ph.F., phloem fibres. × 250.

There still exists in literature much doubt as to whether leguminous nodules are formed partly by the division of deep-seated cortical cells, or whether they are entirely intrastelic in origin. Thornton (1930) in a recent paper on the nodules of lucerne, expresses the opinion that both types are likely to occur.

It is undoubtedly the case in *Viminaria* that at least that part of the nodule external to the vascular strands is cortical in origin, because in young nodules whose phellogen has not yet joined up with that of the root, the endodermis can still clearly be seen, intact, below the cells composing the outer cortical region of the nodule (Text-fig. 18).

A feature of a great majority of the nodules of *Viminaria* is that the vascular strands arise from two or even three separate protoxylem poles of the parent root. This characteristic does not seem to have been reported for any other type of leguminous plant.

Discussion.

a. *Negatively Geotropic Roots.*

Clements (1921, p. 38), in a comprehensive summary of literature dealing with root growth, has come to the conclusion that the development of negatively geotropic roots is a type of aerotropic response by plants grown under conditions of poor soil aeration due to the high water content.

Cases of such root development are by no means rare: numbers of plants habitually develop pneumatophores; others which normally grow in well aerated soil, do so when the soil is saturated. The mangrove vegetation, which grows in saline, airless mud, includes the classic and most consistently pneumatophore-producing types. *Sonneratia* and *Avicennia* (Goebel, p. 278) produce such upright breathing roots; others, *Aegiceras* for example, have "knee-bend" pneumatophores. The phenomenon is not limited to Angiosperms: the Gymnosperm *Taxodium distichum*, when growing in saturated soils, develops short club-like upgrowths and "knee-bends" which are supposed to serve as breathing organs. In the foregoing examples the roots are fairly stout structures with an extensive development of secondary wood.

Jost (1887, p. 601) describes the much less massive negatively geotropic roots produced by *Cyperus*, *Richardia*, *Musa*, and *Papyrus*, when grown in glasshouses, and believes that such breathing organs are widely distributed in the plant world. Several species of *Jussiaea* are also known to produce aerotropic rootlets.

Other plants which do not produce definite pneumatophores, e.g., *Alnus* and *Fraxinus* develop instead an abundance of fine much branched roots near to the surface of the soil (Jost, 1887). Lately Weaver and Himmel (1930) have found that in water-logged soils, such marsh plants as *Scirpus nodosus* and *Typha latifolia* develop a large number of similar roots which grow upwards to the surface of the water, and there spread out widely and often branch profusely.

Nothing is definitely known concerning the mechanism of aerotropic response; as yet one can only postulate that the absence of oxygen in some way overcomes the action of those stimuli which produce the characteristic geotropic and negatively heliotropic responses of most roots.

b. *Aerenchyma.*

A feature of the anatomy of breathing roots is the production of aerenchyma in their cortical regions. In fact, practically all plants growing under aquatic or semi-aquatic conditions show an extensive development of air spaces; and it is important to note that where there is a species or variety sufficiently adaptable to grow both on unsaturated land and under semi-aquatic conditions, in the latter case there is a much greater development of aerenchyma (Arber, p. 201).

There are two main types of aerenchyma, and between them all possible intergradations are found (Arber, ch. xiv; Haberlandt, p. 441). In the first type the component cells are stellate with air spaces between the arms, in the second type the air spaces are developed between plates of rounded or rectangular cells.

In *Viminaria* the aerenchyma is of an intermediate variety; the cells often show short arm-like prolongations, but the lamellar condition is also approached.

Again we are uncertain why there should be this reaction to conditions of more than adequate soil moisture and less than adequate soil oxygen. In this connection, it is of interest to note that Andrews and Beals (1919) in water culture experiments with *Zea mais* found that the roots of plants growing in unaerated media showed a greater development of intercellular spaces than those which grew in aerated media. This seems to point to diminished oxygen supply as being the important factor in the formation of air space systems.

c. *Secondary Aerenchyma.*

Secondary aerenchyma has been described in species of *Jussiaea* and in several leguminous plants, *Neptunia oleracea* and *Sesbania.* Scott (1888) has described the secondary aerenchyma developed by the aquatic roots of *Sesbania aculeata* as arising from a phellogen which originates by the division of cells immediately outside the endodermis, the first or second row of cortical cells. In *Viminaria* the phellogen originates in the normal fashion in the pericycle, and the endodermis is thrown off, together with the primary cortex, on the development of secondary tissue.

Normally the walls of cork cells become impregnated with suberin soon after they are cut off from the phellogen.

Priestley and Woffenden (1922) have come to the conclusion that the preliminary suberisation of cork cell walls is dependent on the presence of air; their experiments show that at least one of the constituents of suberin, phellonic acid, can be taken into solution readily enough, thus preventing suberisation of cell walls in contact with water.

When phellogen activity takes place in a root of *Viminaria* it would appear likely that some of the constituents of suberin go into solution in the surrounding water, and the cell walls of the secondary tissue remain of unimpregnated cellulose and are therefore extensible. If, for a short while, the water level fell and the environment were temporarily drier, the fatty acids released from the protoplasm of the young cork cells would undergo condensation in the absence of an excess of water, and cork layers of varying width would be formed according to whether the period of dryness were long or short.

This explanation gains support from the irregularity with which the layers of cork sometimes arise. When, for instance, a ring of cork is thicker, and at the same time nearer to the phellogen on the upper side of a horizontal root than on the under side, and at the same time the aerenchyma of the ring outside the cork band is wider on the under side, that would indicate a slow fall in water level affecting first the uppermost phellogen derivatives and gradually extending its effect round to the lower ones. If the ring of aerenchyma within the cork band were thicker on the under side, that would indicate a slow rise in water level causing the formation of aerenchyma first on the lower side and then on the upper side of the root. Text-figure 13 indicates that an abrupt rise took place in water level to L, with consequent formation of aerenchyma in the lower part while in the upper part cork formation is still going on. The fluctuations in water level which would be necessary to produce these changes would be quite small.

These results as thus interpreted lend support to Arber's statement (p. 194) that the structure of secondary air containing tissues "is directly induced by environmental conditions, and their serving any purpose is to be regarded as quite fortuitous".

Summary.

1. *Viminaria denudata* Sm., a leguminous shrub growing normally in fairly well aerated soils, can survive a condition of soil saturation for extended periods; it reacts to these conditions in definite ways: *a.*—By the production of both upright and "knee-bend" pneumatophores or breathing roots, in whose parenchymatous tissue an extensive aerating system is present. *b.*—By the production of a secondary aerenchyma in submerged roots which is cut off from a phellogen arising in the pericycle, replacing the cork layers of the normal root.

2. Bacterial nodules may also have a covering of secondary aerenchyma except at their growing points. A nodule may arise in one of two ways: *a.*—By the infection of secondary cortical tissue which is pushed up in a collar round the base of a young lateral root where it arises from its parent root. In this case the nodule is covered from the beginning by a secondary aerenchyma developed from the phellogen of the old root. *b.*—Normally by infection of the cortex of a young root. In this case a phellogen arising round the periphery of the growing nodule becomes continuous with that of the parent root by division of endodermal cells in a position just below the phellogen of the young nodule.

3. Occasional rings of cork of varying width may occur between the zones of secondary aerenchyma in the secondary tissue developed from the phellogen; these are believed to be formed during periods of relatively less soil saturation.

In conclusion, I wish to thank Professor Osborn, of the Department of Botany, University of Sydney, for the interest he has shown during the progress of the work, and for his helpful criticism.

Literature Cited.

Andrews, F. M., and Beals, C. C., 1919.—The Effect of Soaking in Water and of Aeration on the Growth of *Zea mais*. *Bull. Torrey Bot. Club*, 46, pp. 91-100.

Arber, Agnes.—Water Plants.

Clements, F. E., 1921.—Aeration and Air-Content. The Rôle of Oxygen in Root Activity. *Carnegie Inst. Washington*, Publication No. 315.

Goebel, K.—Organography of Plants. Part ii, p. 278.

Haberlandt, G.—Physiological Plant Anatomy.

Jost, L., 1887.—Ein Beitrage zur Kentniss der Athmungsorgane der Pflanzen. *Bot. Zeitung*, 1887, p. 601.

Priestley, J. H., and Woffenden, Lettice M., 1922.—Physiological Studies in Plant Anatomy. V. Causal Factors in Cork Formation. *New Phyt.*, xxi (5), p. 252.

Scott, D. H., 1888.—On the Floating Roots of *Sesbania aculeata* Pers. *Ann. Botany*, i, p. 307.

Thornton, H. G., 1930.—The Early Development of the Root Nodule of Lucerne (*Medicago sativa* L.). *Ann. Botany*, xxiv (clxxiv), pp. 385-393.

Weaver, J. E., and Himmel, W. J., 1930.—Relation of Increased Water Content and Decreased Aeration to Root Development in Hydrophytes. Plant Physiology, V, pp. 69-92.

EXPLANATION OF PLATE XXII.

Fig. 1.—Upright pneumatophores of *Viminaria denudata* growing under natural conditions.

Figs. 2, 3.—Horizontal roots with "knee-bend" pneumatophores (K), upright secondary pneumatophores (P), and absorbing roots (A).

Fig. 4.—Upper part of a primary upright pneumatophore (P), with lateral pneumatophores (P.L.), and young bunches of secondary roots (S).

Fig. 5.—Horizontal root with upright secondary pneumatophores (P), of which the three on the left are the younger, the pneumatophore on the extreme right has given rise to a young lateral (P.L.).

Fig. 1 × ¼ approx.; figs. 2-5 × ½.